Prey-specific capture behaviour and prey preferences of myrmicophagic and araneophagic jumping spiders (Araneae: Salticidae)

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Prey-specific capture behaviour and prey preferences of myrmico-phagic and araneophagic jumping spiders (Araneae: Salticidae). - As prey for salticids, ants and spiders both can be dangerous. Not surprisingly, these dangerous prey appear not to dominate the diet of most salticid species. However, an interesting minority of salticid species routinely preys on either ants (`myrmicophagic salticids') or spiders (`araneophagic salticids'). We review recent work on two facets of behavioural specializ-ation in myrmicophagic and araneophagic salticids: prey-specific capture behaviour and prey preferences. We suggest that predators evolving prey-specific capture behaviour against dangerous prey also tend to evolve distinctive preferences for these dangerous prey. Exceptionally acute eyesight, made possible by the unique, complex eyes of salticids, has probably facilitated the evolution of pronounced prey-specific capture behaviour and prey preferences in these spiders.

Key-words: Spiders - salticids - specialization - capture behaviour - prey preference - myrmicophagy - araneophagy

INTRODUCTION

The Salticidae is a large (over 4000 described species) and diverse family of spiders (CODDINGTON & LEVI 1991) with unique, complex eyes and acute vision (LAND 1969a, b; BLEST et al. 1990). The typical prey of salticids tend to be soft-bodied, more or less safe insects such as flies, and acute vision probably enables salticids to avoid contacting potentially dangerous prey. However, in this paper, we consider salticids that specialize on potentially dangerous ants and spiders (NENTWIG 1986), prey that are rarely dominant in the diet of most salticid species. However, an

interesting minority of salticid species routinely preys on either ants ('myrmicophagic salticids') or spiders ('araneophagic salticids') (RICHMAN & JACKSON 1992). In the present paper, we review recent work on two facets of behavioural specialization in myrmicophagic and araneophagic salticids: prey-specific (*i.e.*, specialized) capture behaviour and prey preferences. However, because the term "specialized" has been applied to both a predator's diet and its predatory behaviour, it is important to first specify how the term "specialized" is used here.

Stenophagous versus euryphagous predators

The diets of predators are often described as stenophagous or euryphagous and as specialized or generalized, where the terms "stenophagous" and "euryphagous" refer to the breadth of food resource utilization (*e.g.*, MORSE 1971; FOX & MORROW 1981). Predators are considered to be stenophagous if their diets include only a narrow range of prey types (one or a few) and euryphagous if their diets include a wide range of prey types. It is useful to use "stenophagous *versus* euryphagous" to refer to the predator's diet and "specialized *versus* generalized" to refer to the predator's behaviour (see JACKSON & VAN OLPHEN 1991, 1992).

Predators with prey-specific capture behaviours are behaviourally specialized. A stenophagous predator may or may not have evolved prey-specific ("specialized") capture behaviour for use against the few types of prey in its diet. A euryphagous predator might be "specialized" or "generalized" in capture behaviour. That is, an euryphagous predator may use generalized (unspecialized) capture behaviour against the numerous types of prey on which it normally feeds. Alternatively, a euryphagous predator may be "versatile" (CURIO 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each adaptively fine-tuned to a different type of prey in its broad diet. A versatile predator is, therefore, euryphagous in diet but behaviourally a specialist on multiple prey types.

An additional distinction is based on preference for prey types. A predator's prey preference is distinct from its actual diet and also from its capture behaviour. Preference, which implies ability to distinguish between different types of prey and choose one rather than another, cannot be inferred simply from knowing the animal's diet in nature or from knowing that the animal has prey-specific capture behaviour.

Specialization in the Salticidae

Spiders as a group are generally envisaged as more or less euryphagous in diet (BRISTOWE 1941; FOELIX 1982; WISE 1993). Yet, scattered reports in the literature (see NENTWIG 1986) suggest that stenophagy, prey-specific capture behaviour and distinctive preferences for unusual prey may be common. The present review is restricted to the Salticidae, a family that has two groups of species with especially pronounced predatory versatility - ant-eating (myrmicophagic) species and spider-eating (araneophagic) species (RICHMAN & JACKSON 1992).

Detailed information about diet, which depends on field studies, is generally absent from the literature on salticids, but all salticids, including the myrmicophagic and araneophagic species, appear to be more or less euryphagous (EDWARDS *et al.* 1974; JACKSON 1977; CUTLER 1980). The present review, therefore, will concentrate on recent laboratory studies of prey-specific capture behaviour and prey preferences.

PREY-SPECIFIC CAPTURE BEHAVIOUR

FORSTER (1977, 1982) analyzed in detail the visually-mediated hunting sequences prevalent in salticid species. The salticid first orients by swivelling its cephalothorax around to bring the principal (AM) eyes to bear on the prey. Next, it aligns its abdomen with its cephalothorax and begins a pursuit, usually by stalking slowly in an almost cat-like manner, towards the prey. When close, the salticid lowers its body and fastens a dragline to the substrate, pauses, then leaps onto the prey. Although this appears to be the typical predatory sequence for most salticid species, myrmicophagic and araneophagic salticids are exceptions.

Araneophagic salticids

Eating other spiders appears to be an opportunistic occurrence for most spiders, a larger or faster individual overpowering another in a chance encounter, but there are numerous exceptions. Some salticids make a practice of leaping or walking into webs to catch the resident spider (TOLBERT 1975; ROBINSON & VALERIO 1977; JACKSON 1985a, b, 1986, 1988). However, the most extreme specialization on spiders as prey known is in ten species of salticids (from 4 genera), all from the subfamily Spartaeinae (WANLESS 1984). These species practise vibratory aggressive mimicry in other spiders' webs, where they sometimes capture spiders larger than themselves. In the present review, the term `araneophagic salticids' is restricted to these species (JACKSON 1992a). Each of these species also preys on insects (either in or out of webs), and the Queensland *Portia fimbriata* also preys on other salticids. A large spider (because it is dangerous), another salticid (because it can see well) or a spider in a web (because it is in a special environment - a web) would all seem to be something that a salticid, as a predator, would perceive as special. The most important common factor is probably that these spiders tend to be, for salticids, difficult-to-catch and dangerous potential prey - the potential prey is also a potential predator.

In a web, an araneophagic salticid's strategy is usually not simply to stalk or chase down the resident spider but instead to send vibratory signals across the silk (aggressive mimicry). The resident spider may respond to these signals in a way that appears indistinguishable from how it would respond to a small insect ensnared in the web, but when the duped spider gets close, the araneophagic salticid lunges out and catches it.

The most extensively studied araneophagic salticids are from the genus *Portia*, and in these species aggressive mimicry is combined with pronounced behavioral

complexity (JACKSON & POLLARD 1996). *Portia* has a large repertoire of vibratory signals (JACKSON & WILCOX 1993*a*) made by manipulating, plucking and slapping the silk with one or any combination of its legs and palps, all of which can be moved in different ways. *Portia* also makes signals by flicking its abdomen, and abdominal movements can be combined with all of the appendage movements. Many of these behaviours by which *Portia* makes signals appear to be evolutionary modifications of grooming behaviour (JACKSON & HALLAS 1990).

The web-building spider, *Portia*'s intended victim, has acute abilities to detect and discriminate between vibratory signals transmitted over the silk in its web, but how the spider interprets these web-borne vibrations varies considerably between species and also with the sex, age, previous experience and feeding state of the spider (WITT 1975; JACKSON 1986; MASTERS *et al.* 1986). Yet *Portia* has been observed using aggressive mimicry to catch many kinds of web-building spiders, within a range of about one tenth to twice *Portia*'s size (JACKSON & BLEST 1982*b*; JACKSON & HALLAS 1986a). Preliminary results suggest that the key to *Portia*'s success at victimizing so many different types of spiders is an interplay of two basic ploys: 1) using prey-specific (fixed) signals when cues from some of its more common prey species are detected (JACKSON & WILCOX 1990); and 2) using feedback to adjust signals to different prey species (JACKSON & WILCOX 1993*a*). The first ploy, using fixed tactics, is consistent with the popular potrayal of spiders as animals governed by instinct. With the second ploy, *Portia* solves problems: *Portia* determines, by trial and error, what to do with different victims. Other problem-solving abilities include making detours when approaching prey (JACKSON & WILCOX 1993*b*; TARSITANO & JACKSON 1993, 1994) and smokescreen behaviour (WILCOX *et al.* 1996).

A number of spider species from several families other than the Salticidae are also web-invading araneophagic spiders that use aggressive mimicry (JARMAN & JACKSON 1986; JACKSON & WHITEHOUSE 1986; WHITEHOUSE 1986; JACKSON & BRASSINGTON 1987). However, web-invading araneophagic salticids appear to differ in important ways from the web-invading araneophagic spiders of other families. Araneophagic salticids can walk across both ecribellate and cribellate sticky webs without getting stuck (JACKSON 1986), and they are highly effective at preying on a wide array of web-building spiders. In contrast, none of the araneophagic non-salticid spiders studied can cross both cribellate and ecribellate sticky webs unimpaired. Also, the set of web-building spiders caught by araneophagic non-salticid spiders is considerably smaller than that of the araneophagic salticids, and the predatory strategies of the araneophagic non-salticid spiders appear to be less complex than those of the araneophagic salticids (JACKSON 1992*a*). Signal output variation appears important in enabling both salticid and non-salticid aggressive mimics to achieve fine control over the responses of each particular victim spider. However, compared to the araneophagic non-salticid spiders, the araneophagic salticids use a larger repertoire of vibratory signals and they combine and vary their signals more extensively. Unlike the araneophagic non-salticid spiders, the araneophagic salticids have acute vision (JACKSON & BLEST 1982*a*) and are not restricted to interpreting web vibrations when detecting, identifying, and locating prey on webs. The absence of acute vision may

have been an important constraint limiting the range of prey taken by the araneophagic non-salticid spiders (JACKSON 1986, 1992*a*).

Although not so extensively studied as *Portia*, the other aggressive-mimic salticids (*Brettus*, *Cyrba* and *Gelotia*) also readily invade many different types of webs and also resemble *Portia* by using strategies based on a combination of fixed signals and trial-and-error behaviour (JACKSON & HALLAS 1986*c*; JACKSON 1990*a*, *b*). However, the genera of araneophagic salticids differ markedly in the methods used for catching prey. For example, *Brettus*, *Cyrba* and *Gelotia* are generally more inclined than *Portia* to remain near the edge of the web (JACKSON & HALLAS 1986*c*). However, the most well-studied differences are among the species, and even populations of single species of *Portia*.

The most pronounced example of interpopulation difference in predatory behaviour is the Queensland population of *P. fimbriata*, which differs from all other *Portia* studied by having special methods for catching cursorial salticids belonging to other genera. *P. fimbriata*'s habitat in Queensland is unique among those studied in having an abundance of cursorial salticids (JACKSON & HALLAS 1986*a*) and, apparently, the Queensland *P. fimbriata*'s predatory behaviour is specially adapted to this locally abundant type of prey (JACKSON 1992*b*).

In the open, the Queensland *P. fimbriata* uses cryptic stalking, a special kind of trickery, but not an example of aggressive mimicry (JACKSON & BLEST 1982*b*). The Queensland *P. fimbriata*, in common with all *Portia*, has an unusual (cryptic) appearance; because of markings, tufts of hairs, and long, spindly legs, *Portia* resembles a piece of detritus and a slow, choppy gait probably helps a moving *Portia* preserve detritus resemblance. Crypsis, which probably provides *Portia* with protection against its own visually hunting predators, is also important in relation to cryptic stalking. When cryptically stalking a salticid, *P. fimbriata* moves especially slowly, pulls its palps back and out of its prey's view, and freezes if the salticid turns to face it, thereby concealing itself from this special type of prey spider which, in common with *Portia*, has acute eyesight. Eventually, the Queensland *P. fimbriata* approaches the salticid from behind, then swoops down to kill it. In addition, the Queensland *P. fimbriata* is unique among *Portia* studied because it makes vibratory signals on the nests of salticids to entice them out and catch them (JACKSON & HALLAS 1986*a*). Furthermore, the Queensland *P. fimbriata* has a special tactic for catching *Euryattus*, a salticid sympatric with the Queensland *P. fimbriata*, but not sympatric with any other *Portia* studied: the Queensland *P. fimbriata* mimics the unique courtship signals of *Euryattus* males to lure *Euryattus* females out of suspended rolled-up leaves and attack them (JACKSON & WILCOX 1990).

Myrmicophagic salticids

Ants come equipped with strong mandibles, poisonous stings and formic acid (EISNER 1970; BLUM 1981). Also, being social insects, ants tend to be present in large numbers and can mount communal attacks on predators and prey (WILSON 1971; HOLLDOBLER & WILSON 1990). All of these factors tend to present formidable

challenges to most cursorial spiders (NENTWIG 1986). However, in most terrestrial environments, and especially in the tropics (where salticids appear to be the dominant spider family: (BRISTOWE 1941), ants are the dominant arthropods in the size range of the prey normally taken by salticids (HOLLDOBLER & WILSON 1990). For a salticid that overcomes the ant's defence, a rich food resource becomes available.

Ants and certain other arthropod groups (*e.g.*, bees, wasps, carnivorous bush-crickets, etc.) present salticids with a problem similar to spiders as prey: they are unusually difficult-to-catch and dangerous, and apparently one of the most effective ways for salticids to exploit ants is with specialized (*i.e.*, prey-specific) capture be-haviour. Also, for ants, as for spiders, apparently only a minority of salticid species routinely preys on these heavily defended prey (see ROBINSON & VALERIO 1977). The capture behaviour of 9 myrmicophagic salticid species (6 belonging to subfamily Heliophaninae and 3 to subfamily Euophrynae) has been studied in detail and each of these 9 species preys not only on ants but also on other (more conventional) prey insects (*e.g.*, flies). Each has evolved prey-specific capture behaviour for use against ants, which differs from the predatory behaviour they use to capture other insects (EDWARDS *et al.* 1974; CUTLER 1980; WING 1983; JACKSON & VAN OLPHEN 1991, 1992; JACKSON & POLLARD 1996; LI *et al.* in press).

Predatory behaviour used against ants varies among the species, but the six heliophanines are remarkably similar to each other, while differing from each of the three euophrynes. Among the euophrynes, *Zendorus* (formerly *Pystira*) *orbiculata* differs considerably in behaviour from another two euophrynes, *Corythalia canosa* (JACKSON & VAN OLPHEN 1991) and *Habrocestum pulex* (LI *et al.*, in press). *C. canosa* and *H. pulex* resemble each other by manoeuvring to attack the ant head on. However, unlike *C. canosa*, *H. pulex* never holds its body raised while pursuing, attacking and starting to feed on ants. *Z. orbiculata* attacks ants from just about any orientation. However, *Z. orbiculata*, unlike the other myrmicophagic salticids, also often positions itself facing down on ant-infested tree trunks and ambushes ants by lunging down on them instead of actively pursuing them. *H. pulex* resembles the heliophanines by often stabbing ants then backing away. However, *H. pulex* usually attacks ants head-on. The heliophanines (JACKSON & VAN OLPHEN 1992) sometimes attack ants head on, but they also often attack from directly behind the ant. Not only do all these species stab the ant and attack from directly behind it, but they also usually hold legs I elevated while pursuing, attacking and starting to feed on ants. In contrast, *C. canosa* (JACKSON & VAN OLPHEN 1991) tends to hold its cephalothorax, but not its legs I, elevated.

PREY PREFERENCES OF SPECIALIZED SALTICIDS

We ask three questions about araneophagic and myrmicophagic salticids: 1) Do the species with prey-specific capture behaviour for catching dangerous prey (*i.e.*, ants and spiders) prefer these dangerous prey? 2) Do these species prefer certain sizes of prey? 3) Do males and females of these species prefer the same prey?

Testing methods

NENTWIG (1986) investigated the prey preferences of a wide variety of spiders using different types of prey presented sequentially, and he found evidence of selectivity. A similar method used in an early study of *Portia*'s prey preferences (JACKSON & HALLAS 1986*a*) found that *Portia* preferred spiders to insects as prey. Also, there have been three prey-preference studies of *Phidippus audax*, a common North American salticid: each found evidence of selective predation when different prey were presented simultaneously (GIVENS 1978; FREED 1984; ROACH 1987).

However, the studies we now review differ from the above studies of prey preferences: for each species reviewed here, three distinct types of tests for prey preference were carried out (JACKSON & VAN OLPHEN 1991) - 1) one individual of one type of prey presented to a predator at a time on alternate days, sequence decided randomly; 2) two types of prey presented to a predator simultaneously, one individual prey of each type; and 3) feeding predator presented with one individual of an alternative prey type, sequence for alternate days decided randomly. A strength of these testing routines is that, for each salticid species tested, findings from the different test designs can be compared for consistency. Consistent evidence of the same preference across test designs makes conclusions especially convincing.

Taxonomic categories of prey preferred

Each of 9 species of myrmicophagic salticids studied not only uses a prey-specific behaviour for catching ants, and a different prey-specific behaviour for catching other insects, but also has a distinct preference for ants over other varied types of prey as demonstrated by consistent results across Type 1 - 3 tests (JACKSON & OLPHEN 1991, 1992; LI *et al.* in press).

All of the araneophagic salticids that are known to have prey-specific behaviour for catching spiders (*i.e.*, *Brettus*, *Cyrba*, *Gelotia* & *Portia*) also appear to prefer spiders to insects as prey (JACKSON 1992*a*). However, information from detailed studies based on Type 1 - 3 tests is available only for *Portia fimbriata* from Queensland (LI & JACKSON, in press) and *Portia labiata* from Sri Lanka (Li & Jackson, unpubl. data). These studies show that *P. fimbriata* and *P. labiata* are behaviourally specialized as predators on web-building spiders in two distinct ways: besides using prey-specific capture behaviour against web-building spiders (JACKSON 1992*a*), consistent results from Type 1 - 3 tests show that they also have pronounced preferences for web-building spiders to insects (LI & JACKSON, in press).

Queensland *P. fimbriata* are of special interest because of the unusual component of this *Portia*'s diet: they frequently eat other species of salticids in nature (JACKSON & BLEST 1982*b*). Remarkably, not only does the Queensland *P. fimbriata* use specialized prey-catching behaviour against the salticids on which it preys, but also, from consistent results across Type 1 - 3 tests show that they prefer salticids to other spiders as prey (LI & JACKSON, in press). The Queensland *P. fimbriata* appears to have a hierarchy of prey preferences: on a broader scale, it prefers spiders (both cursorial

salticids and web-building spiders) over insects; on a finer scale, it prefers cursorial salticids over web-building spiders.

Portia labiata and the Queensland *P. fimbriata* are behaviourally different because there is no evidence that *P. labiata* uses cryptic stalking or any other prey-specific capture behaviour against cursorial salticids and, in contrast to the Queensland *P. fimbriata*, *P. labiata* is decidedly ineffective at catching cursorial salticids (JACKSON & HALLAS 1986*a*, *b*). The contrast between *P. labiata* and Queensland *P. fimbriata* extends also to prey preferences: results from Type 1 - 3 tests showed that *P. labiata* prefers web-building spiders to cursorial salticids (Li & Jackson, unpubl. data). Evidently, local abundance of cursorial salticids has also shaped the evolution of, not only salticid-specific capture behaviour, but also prey preferences.

The biology of the myrmicophagic and araneophagic salticids studied suggests that, when predators evolve prey-specific capture behaviour for use against dangerous prey, they also tend to evolve distinct preferences for these dangerous prey. Why this might be so is not obvious. Detailed comparative studies of non-salticid predators are needed to clarify how broadly applicable this trend is in animals.

Males and females compared

In nature, males of all species of *Portia* studied resemble females by frequently feeding on web-building spiders (JACKSON & BLEST 1982*b*; Jackson, unpubl. data). Also, males of all species of *Portia* studied use the same prey-specific prey-catching behaviours against web-building spiders as females (JACKSON & BLEST 1982*b*; JACKSON & HALLAS 1986*a*). In the laboratory, an additional similarity has been illustrated: in Type 1 - 3 tests, both the males and the females of the Queensland *P. fimbriata* (LI & JACKSON, in press) and the Sri Lanka *P. labiata* took web-building spiders in preference to insects as prey (Li & Jackson, unpubl. data).

Furthermore, males of the Queensland *P. fimbriata*, in common with females, frequently prey on cursorial salticids (JACKSON & BLEST 1982*b*; Jackson, unpubl. data) and both males and females also use cryptic stalking against cursorial salticids (JACKSON & HALLAS 1986*a*). Also, in Type 1 - 3 tests, both males and females of the Queensland *P. fimbriata* take cursorial salticids in preference to web-building spiders as prey (LI & JACKSON, in press). In contrast, in Type 1 - 3 tests, both males and females of the Sri Lanka *P. labiata* take web-building spiders in preference to cursorial salticids as prey (Li & Jackson, unpubl. data).

Females of spiders appear to have evolved a lifestyle that emphasizes the consumption of large quantities of food as an adaptation for adding yolk to eggs. Males, in contrast, appear to have evolved a lifestyle emphasizing courtship, mating, and searching for females (see VOLLRATH & PARKER 1992). Because male lifespan is generally short and food requirements are smaller than for females, a preference by males for prey smaller than that preferred by females might be expected. Evidence of this difference was first demonstrated for *Phidippus audax*, a common North American and predominantly insectivorous salticid: *P. audax* males tend to take smaller

prey than females (GIVENS 1978). A similar interspecific difference was found in the Queensland *P. fimbriata*: in Type 1 - 3 tests, males Queensland *P. fimbriata* took smaller spiders (both web-building spiders and cursorial salticids) than did females (LI & JACKSON, in press).

Effect of hunger on prey-preference behaviour

Although hunger has numerous influences on the behaviour of predators (CURIO 1976), including salticids (DREES 1952; GARDNER 1964), little is known about how hunger affects the prey-preference behaviour of salticids. Recently, hunger was investigated in araneophagic and myrmicophagic salticids and found to vary among the species studied. In *Corythalia canosa, Chrysilla lauta, Natta* spp. and *Siler semiglaucus* (JACKSON & VAN OLPHEN 1991, 1992), well-fed individuals had distinct preferences for ants, but these preferences broke down when these myrmicophagic salticids had been starved for two weeks before testing. When starved, these ant-eating species took ants and other insects indiscriminately. However, prey preferences of myrmicophagic *Habrocestum pulex* (LI *et al.*, in press), and araneophagic *P. fimbriata* (LI & JACKSON, in press) and *P. labiata* (Li & Jackson, unpubl. data), were not affected by a 2-week period without food. Why hunger influences these species differently is currently unclear.

THE ROLE OF VISION IN PREY-PREFERENCE BEHAVIOUR

The distinguishing characteristic of salticid spiders is their complex eyes (LAND 1974; FORSTER 1982; BLEST & CARTER 1987; BLEST *et al.* 1990). The principal eyes are responsible for acute vision (HOMANN 1928; LAND 1969*a, b*, 1971), allowing the salticid to identify mates, rivals and predators from distances of 30 body lengths or more (JACKSON & BLEST 1982*a*; Jackson, unpubl. data). Exceptionally good eyesight has probably facilitated the evolution of pronounced preference behaviour in these spiders: evidently, these salticids can discriminate, prior to contact, between different types of prey (JACKSON & BLEST 1982*a*).

The cues used by typical salticids for distinguishing between insect prey and other objects such as mates, rivals, enemies and irrelevant stimuli, have been investigated extensively. Shape, symmetry, presence of legs and wings, size, and style of motion (short, jerky movements) are some of the more important features by which these salticids appear to recognize their prey (HEIL 1936; CRANE 1949, DREES 1952; FORSTER 1979, 1982; EDWARDS 1980). However, for salticids with predatory versatility and pronounced prey preferences, we have little information about the cues that influence the various components of the complex predatory strategies. Most of what we know concerns the cues that govern *Portia*'s decisions of whether to enter a web, whether to make signals once in a web, and whether to persist at signalling once started. Seeing a web elicits web entry, but volatile chemical cues from webs of prey spiders do not appear to be important. Seeing a spider in a web increases *Portia*'s

inclination to enter the web. After web entry, cues from the web are sufficient to elicit signalling behaviour, even in the absence of other cues coming directly from the prey spider. Seeing a prey spider or detecting vibrations on the web make *Portia* more prone to signal, but volatile chemical cues from the prey spiders themselves do not appear to be important. Once *Portia* is on a web and signalling, seeing a moving spider and detecting vibrations on the web encourage *Portia* to persist in signalling (JACKSON 1995).

Prey movement is an especially effective stimulus for eliciting orientation and pursuit by typical salticids (DREES 1952; DILL 1975). Different patterns of movement may also permit salticids to distinguish between different types of prey (FREED 1984). However, movement is not always necessary. Anecdotal evidence suggests that typical insectivorous species of salticids occasionally stalk and attack motionless prey (see FORSTER 1985), and *Portia* preys readily on quiescent web-building spiders in nature and in the laboratory (JACKSON & HALLAS 1986a). Additionally, in the laboratory *Portia* can distinguish between quiescent spiders, insects and eggsacs using visual cues alone (JACKSON 1995). Also, eleven salticid species, including *Corythalia canosa* (a myrmicophagic salticid) and four species of *Portia* (araneophagic salticids), stalk and attack completely motionless (dead) prey. The myrmicophagic and araneo-phagic salticids used the same prey-specific capture behaviour with the different kinds of motionless prey that they normally used with the same kinds of living prey (JACKSON & TARSITANO 1993). Also, the prey preferences of two species of araneo-phagic salticids, the Queensland *P. fimbriata* (LI & JACKSON, in press) and *P. labiata* (Li & Jackson, unpubl. data), and one species of myrmicophagic salticid, *Habro-cestum pulex* (LI *et al.*, in press), have been investigated in tests using dead, motionless prey and shown to be the same as in tests using living prey. These studies suggest that cues from prey shape alone are sufficient to elicit prey-specific capture behaviour and prey preferences in salticids.

DREES (1952), in an experimental study using *Evarcha plancardi*, used lures to investigate the cues by which this insectivorous salticid distinguishes between prey (insects, to be attacked) and other salticids (mates or rivals, to be displayed at). He found that an effective model for evoking conspecific displays had to have a central "body" and a series of `legs' on each side, with the legs making appreciable angles. More legs made lures more effective at eliciting displays. In contrast, lures taking a wide variety of forms were effective at eliciting attacks as long as they moved and were not appreciably larger than the salticid. DREES' (1952) experiments suggest that the insectivorous salticid's rule is: "if it moves, find out whether it has legs in the right places; if it does, display; if it does not, try to catch it". However, for myrmicophagic and, especially, araneophagic salticids, the rules must be considerably more complex. The Queensland *P. fimbriata* is perhaps the most complex, as it preys not only on other spiders but also on other species of salticids. The cues by which myrmicophagic and araneophagic salticids distinguish between different types of prey are currently being investigated.

Questions about the cues used by salticids with predatory versatility highlight how far we remain from fully understanding the functioning of the salticid visual

system. Although salticid eyes are large and complex for a spider, this is no primate (LAND 1974). The principal eye lens is only a few millimetres in diameter, and there are only a limited number of receptors in the salticid eye and neurons in the salticid brain. How so small a visual system, with so few components, is able to perform these perceptual feats is currently a mystery.

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